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CIRCULATION OF FLUIDS IN THE GASTROVASCULAR SYSTEM OF THE REEF CORAL *ACROPORA CERVICORNIS*

ELIZABETH H. GLADFELTER

West Indies Laboratory, Teague Bay, Christiansted, St. Croix, USVI 00820, and Department of Biology, University of California, Los Angeles, California 90024

Abstract

Circulation of fluids in the gastrovascular system of *A. cervicornis* was determined by observing the movement of fluorescein dye injected via a lateral polyp and viewed in the dark under ultra-violet light. Scanning electron microscopy and petrographic thin sections were used to describe the general morphology of the gastrovascular system. This consists of two functional units: an axial unit composed of the coelenteron of the axial polyps and a peripheral unit composed of tubes oriented axially ramifying through the skeleton lying just beneath the outer ectoderm. These units are connected by radially oriented tubes including the coelenterons of the lateral polyps. The entire gastrovascular system is lined by flagellated endoderm cells.

Flow in the axial unit is always proximal. Flow in the peripheral unit is both distal and proximal and the velocity is always less than the flow in the axial unit. Light does not appear to change the rate of flow. Rates of flow in the peripheral unit show a diel cycle, with increased flow rates occurring between 2100 and 0600.

Introduction

Reef corals are symbioses between colonial cnidarians (Anthozoa: Scleractinia) and intracellular dinoflagellates (=zooxanthellae). The animal colony consists of polyps connected by coenosarc through which extensions of the gastrovascular system ramify (Wells, 1956). Thus, there exists the potential for transport of materials (*e.g.*, dissolved or particulate organic matter) from one site in the colony to another.

Gastrovascular transport systems in Cnidaria have been investigated in hydromedusae (Roosen-Runge, 1967); hydroids (Rees *et al.*, 1970); pennatulids (Musgrave, 1909; Parker, 1920; Brafield, 1969); and gorgonians (Murdock, 1978a, b). To date, work on transport in scleractinian corals is limited to a few studies in which materials introduced at one site in the colony have been detected at another site (Pearse and Muscatine, 1971; Taylor, 1977).

The reef coral *Acropora cervicornis* is a branching form consisting of a relatively large axial corallite and polyp at the terminus of each branch, and many smaller lateral calices with polyps along the length of the branch. The distal portion of the axial corallite is a site of rapid skeletal development (*e.g.*, Goreau and Goreau, 1959; Pearse and Muscatine, 1971; Gladfelter, 1982, 1983) and cell division (Gladfelter, 1983); both processes occur in a characteristic diel pattern (Gladfelter, 1983). When soluble organic molecules and $^{45}Ca^{++}$ have been introduced at a distance from the tip of a branch, they have been detected later in the tissues of the axial polyp and its skeleton at the extreme distal portion of the branch; it has been inferred that these molecules and ions have been transported in some way to the tip (Pearse and Muscatine,

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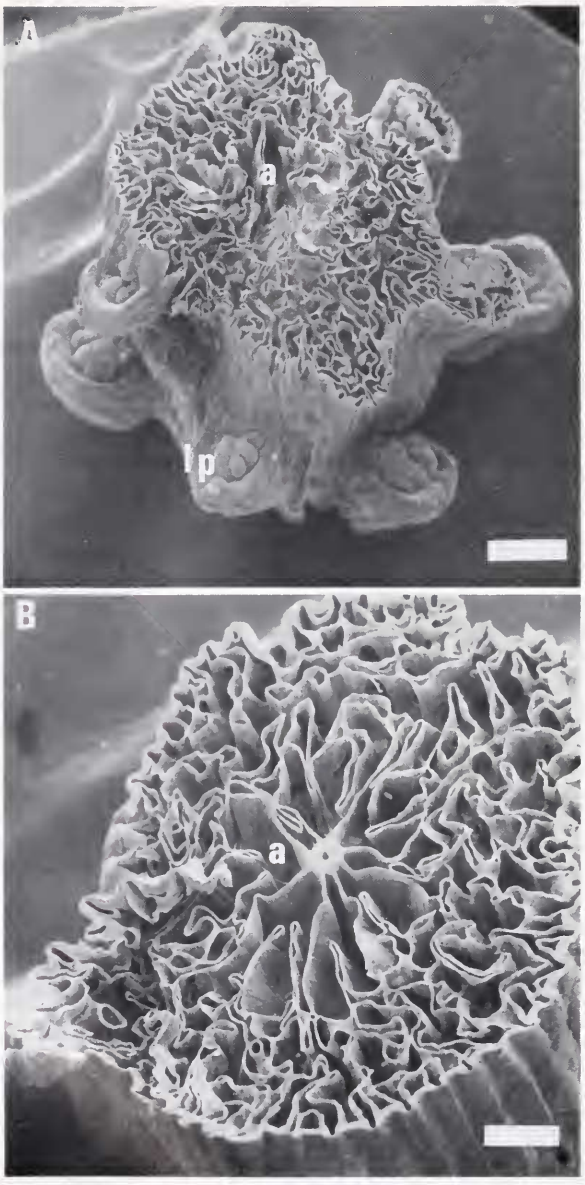


FIGURE 1. Several SEMs of decalcified axial polyps, showing the axial unit of the fluid transport system. a. Cross-section of an axial polyp *ca.* 10 mm from the tip, exposing the axial unit (a) of the fluid transport system, the canal formed by the coelenteron of the axial polyp lying within the calyx of the skeleton. A number of lateral polyps (1p) can be seen. Scale bar = 500 μm. b. Cross-section of the axial polyp *ca.* 20 mm from the tip, showing the now partly occluded axial canal (a). Scale bar = 250 μm. c. View of the membrane surface of the endodermal cells lining the axial canal. Note that each flagellum is surrounded by a circlet of raised projections of the cell membrane. Scale bar = 5 μm.

1971; Taylor, 1977). To date, however, neither the morphological basis of this transport nor the patterns of flow in this hypothesized transport system have been described. The present study was undertaken with these goals in mind.

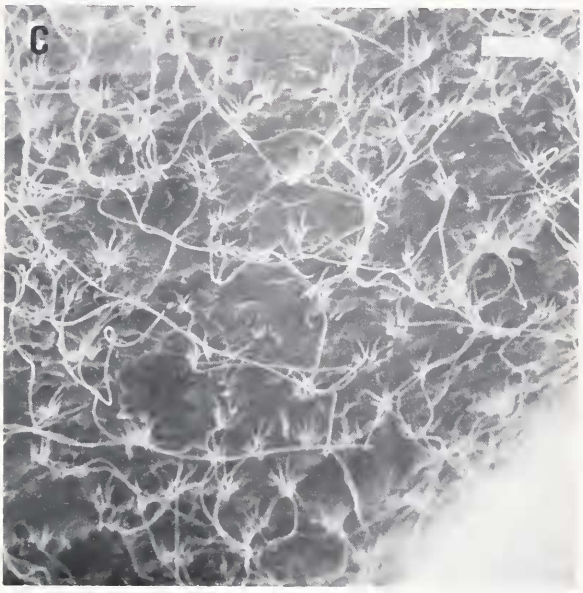


FIGURE 1. (*Continued*)

MATERIALS AND METHODS

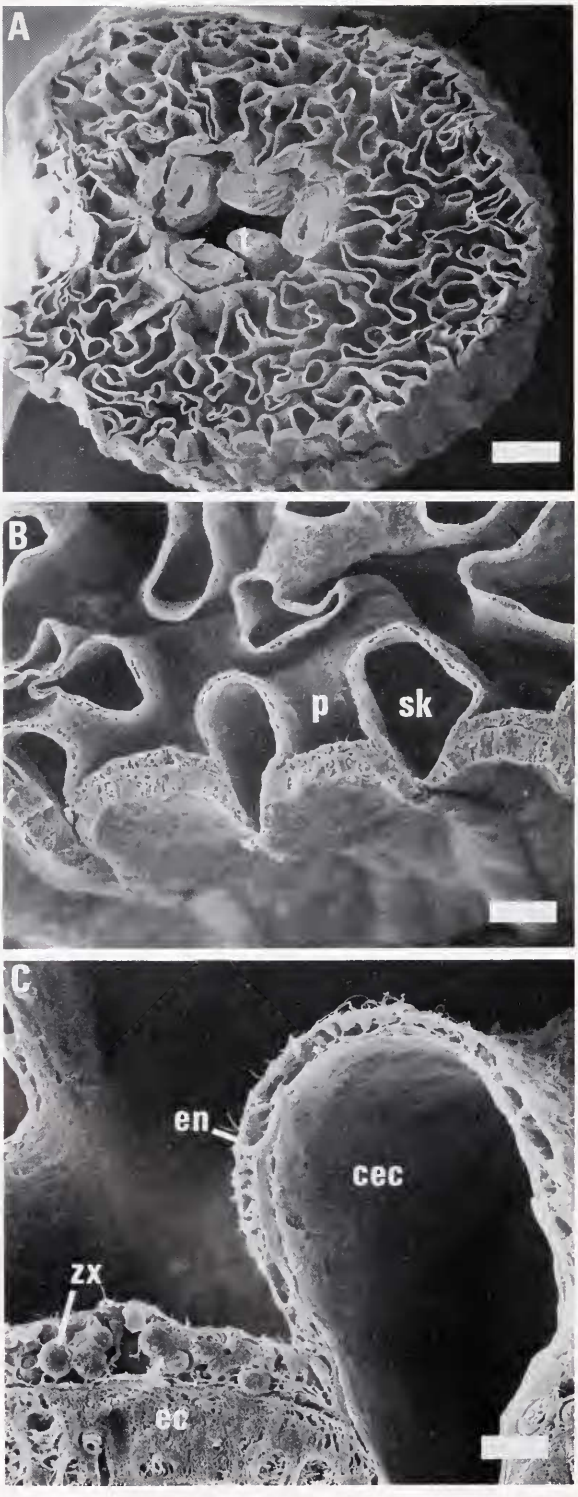
Morphology of the gastrovascular system

Scanning electron microscopy (SEM) was used to describe the general morphology of the gastrovascular system of *A. cervicornis*. Specimens examined by SEM were prepared as described by Gladfelter (1982, 1983). Measurements of the volume occupied by certain parts of the gastrovascular system were made from petrographic thin cross-sections of the skeleton (made along the branch length) as described by Gladfelter (1982); spaces void of skeleton are occupied by the coelenteron of the gastrovascular system (Gladfelter, 1982). The total cross-sectional area of the axial corallite (calyx and theca) and the area of secondary radial growth was determined by direct measurement of 10 colonies (with 2–3 branches per colony).

Patterns and rates of fluid transport

Collection and maintenance of specimens. Acropora cervicornis was collected from a depth of 10–12 m in Buck Island Channel, adjacent to Teague Bay forereef, St. Croix, U. S. Virgin Islands. Straight branches, *ca.* 20 cm long, with a single axial corallite were removed from the colonies. Within 20 min of collection, the branches were transported submerged in a plastic tub filled with sea water to the West Indies Laboratory. The coral branches were placed in shaded outdoor aquaria supplied with fresh continuously flowing sea water. Corals were routinely allowed to acclimate for 24 h before measuring rates of fluid transport.

Detection of fluid transport. The fluorescent dye, fluorescein, was used to detect transport of fluids along the axis of a branch of *A. cervicornis*. For each experiment, 10–12 branches were brought into a darkened laboratory and allowed to acclimate in running sea water for 1 h prior to measurement. The temperature during all the measurements of rates of fluid movement was the same as that of the natural en-


A
t
B
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vironment, 27° ± 1°C. A single branch was placed horizontally in a plastic tub (90 cm × 45 cm × 23 cm) filled with sea water. A hypodermic syringe with a #26 needle was used to inject 0.05 ml of a saturated solution of fluorescein dye in sea water into a lateral polyp. The distance traveled by the moving dye front was measured each minute after the initial injection by observing the branch in the dark with an ultraviolet light. As a control, 3 coral branches were fixed in 10% buffered formalin, injected with fluorescein, and observed as described above. On some coral branches either the distal portion of the axial polyp or the proximal portion of the axial polyp was injected with fluorescein dye, and observed as described above.

Results

Morphology of the gastrovascular system

Canals. The gastrovascular system of a branch of *Acropora cervicornis* is a series of interconnected large (*ca.* 1000 μm in cross-section) and small (*ca.* 100 μm in cross-section) canals. The largest canal in each branch is the portion of the coelenteron of the axial polyp within the calyx of the axial corallite (Fig. 1a, b); this is referred to as the axial canal. Slightly smaller are the somewhat radially oriented canals formed by the coelenterons of the lateral polyps within the lateral corallites. The smallest canals ramify through the porous skeleton (Figs. 2, 3a, b); the canals oriented axially and lying just beneath the outer ectoderm are referred to as peripheral canals. In the distal 5 mm of the branch, the canals within the wall of the axial corallite are the peripheral canals, but as the branch increases in diameter the canals just below the outer ectoderm, between the pseudocostae of the skeleton, serve in this capacity (Fig. 3). Petrographic thin cross-sections of the skeleton were used to determine the cross-sectional areas of component parts of the gastrovascular system. As the branch increases in girth by radial accretion of skeleton, the resulting secondary growth of skeleton contains both the coelenterons of the lateral polyps as well as small canals connecting the axially oriented canals (both peripheral and axial). The total cross-sectional area of the calyx (containing the axial canal) does not decrease significantly until *ca.* 30 cm from the tip, while the cross-sectional area of the combined peripheral canals increases several fold (Table I). The cross-sectional areas of the canals oriented radially, in the secondary radial growth of the skeleton increases from 0 cm^2 at the tip of the branch (where there is no radial growth) to a large cross-sectional area 30 cm from the tip (Table I).

Endodermal cells. The entire gastrovascular system is lined by flagellated endodermal cells (Figs. 1c, 2c, 4, 5). The flagella are *ca.* 200 nm wide and *ca.* 10–15 μm long; they are surrounded by a circlet of *ca.* 10 membrane ridges (Fig. 4a, c) about 1 μm long and up to 200 nm above the surface of the membrane. Each endodermal cell appears to have 1 flagellum (Fig. 5). Zooxanthellae are located primarily in those endodermal cells which lie beneath the outer ectoderm (Figs. 1b, 2c, 5b) although

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FIGURE 2. SEMs of a decalcified axial polyp, exposing a cross-section *ca.* 1 mm from the tip of a branch. a. Low magnification showing the entire axial polyp. The tentacles (t) are withdrawn into space left in the calyx of the corallite. The porous wall (*i.e.*, theca) of the corallite contains the ramifying canals of the peripheral unit of the fluid transport system. Lower edge is magnified in 2b, c. Scale bar = 250 μm. b. The ramifying canals of the peripheral unit (p) are located within the porous skeleton (sk), seen in this view as empty space after the removal of the mineral. Scale bar = 50 μm. c. Enlargement of 2b showing the tissue layers at the edge of the axial polyp: outer ectoderm (ec), calicoblastic ectoderm (cec) and endoderm (en) which contains zooxanthellae (zx). Scale bar = 12.5 μm.

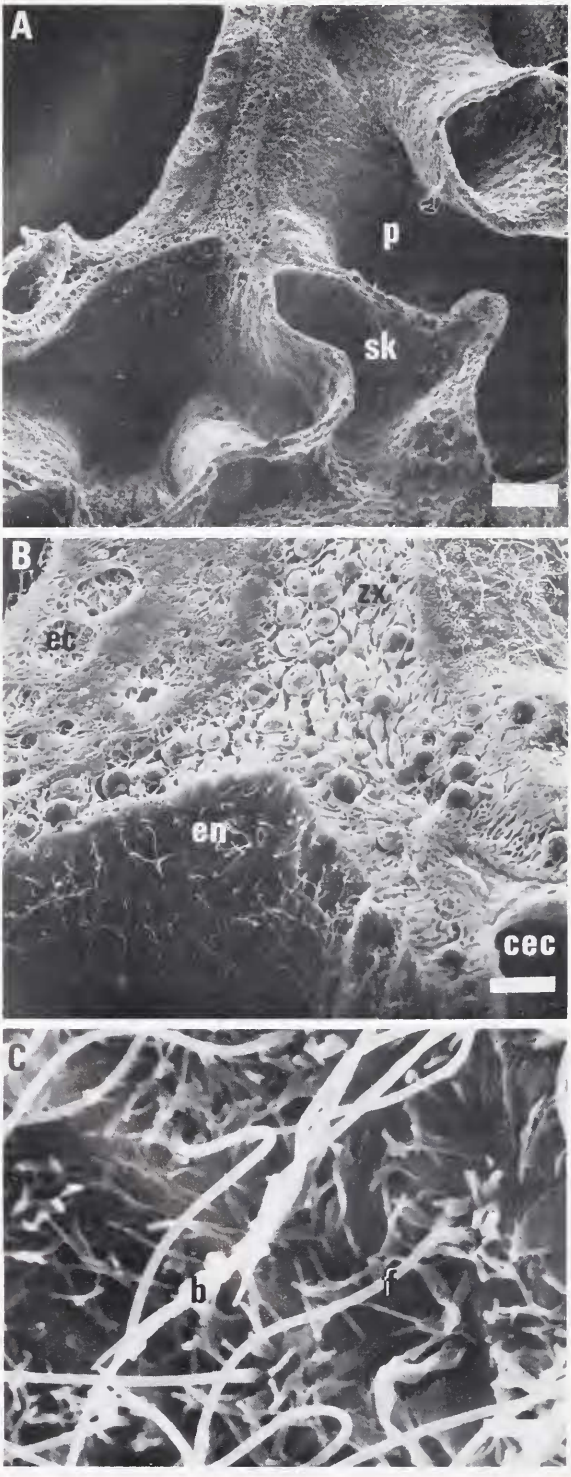
A
p
sk
B
zx
ec
en
cec
C
b
f

TABLE I

Cross-sectional area (cm^2) of the components of the fluid transport system at different distances from the branch tip

Distance from tip (cm)	Axial unit-axial canal	Peripheral unit peripheral canals	Radial unit lateral canals
0	.020	.028	—
10	.016	.074	.30
20	.015	.105	.50
30	.008	.135	.90

occasionally they are found deeper within the colony. There appears to be one zooxanthella per cell (Fig. 5b).

The surface of the endodermal cells facing the coelenteron may have relatively few membrane projections (Fig. 4a) between flagella. However, there may be numerous folds projecting above the surface of the membrane, particularly in those cells containing zooxanthellae and lying adjacent to the outer ectoderm (Figs. 1c, 4c) or endodermal cells in the gastrovascular pockets of the distal portion of the axial polyp in the specimens fixed at night (*i.e.*, either 2400 or 0500; Fig. 4b). The surfaces of cell membranes in specimens fixed during the day (*i.e.*, 1100 and 1800) have fewer projections (Fig. 4a).

Endodermal cells at different sites in the gastrovascular system have different shapes. Cells at the distal tip of the axial corallite, at the distal end of the peripheral canals are columnar, *ca.* 12 μm tall and *ca.* 1 μm in diameter (Fig. 6a). Proximal to the tip, the shape of the endodermal cells becomes squamous (Fig. 6b), only a few μm tall, and *ca.* 10 μm in diameter; by 200 μm below the distal tip, most of the endodermal cells lining the canals of the gastrovascular system have this shape. The exceptions are cells containing zooxanthellae; these cells, lying beneath the outer ectoderm and lining the peripheral canals (Figs. 2c, 3b) are tall (*ca.* 12 μm) and broad (*ca.* 10 μm). There is a large subepidermal space in the endoderm (Fig. 5a, b); it is more noticeable where cells are not occupied by zooxanthellae.

The distal end of a peripheral canal has a high density of flagella. This is due to the columnar shape of the cells, with a correspondingly small membrane surface (containing one flagellum per cell) facing the coelenteron (Fig. 7).

In this study the digestive role of the gastrovascular system was not investigated; nevertheless, certain observations can be made from SEMs. As noted above, numerous projections, microvilli, often vastly increase the surface area of the endodermal cell membrane. Foreign particles were found in contact with these microvilli (Fig. 4b, c). In several SEM preparations, particulate matter was present in the canals of the gastrovascular system. In one case the particulate matter was a mass of unidentifiable smaller particles (perhaps partially decomposed food) entangled by flagella (Fig. 7a,

FIGURE 3. SEMs of the outer edge of a decalcified branch, exposing a tangential section located 45 cm from the tip. a. View of peripheral canals (p) between pockets left after the dissolution of the pseudocostae of the skeleton (sk). Scale bar = 50 μm. b. Higher magnification of 3a, showing the configuration of the tissue layers at the edge of the branch, labeled as in Figure 2. The label, en, is located in the approximate region magnified in 3c. Scale bar = 12.5 μm. c. View of the membrane surface of endodermal cells lining the coelenteron. Note the flagella (f) and numerous small projections of the membrane surface. Small particles, possibly bacteria (b) are also seen on the surface. Scale bar = 1.3 μm.

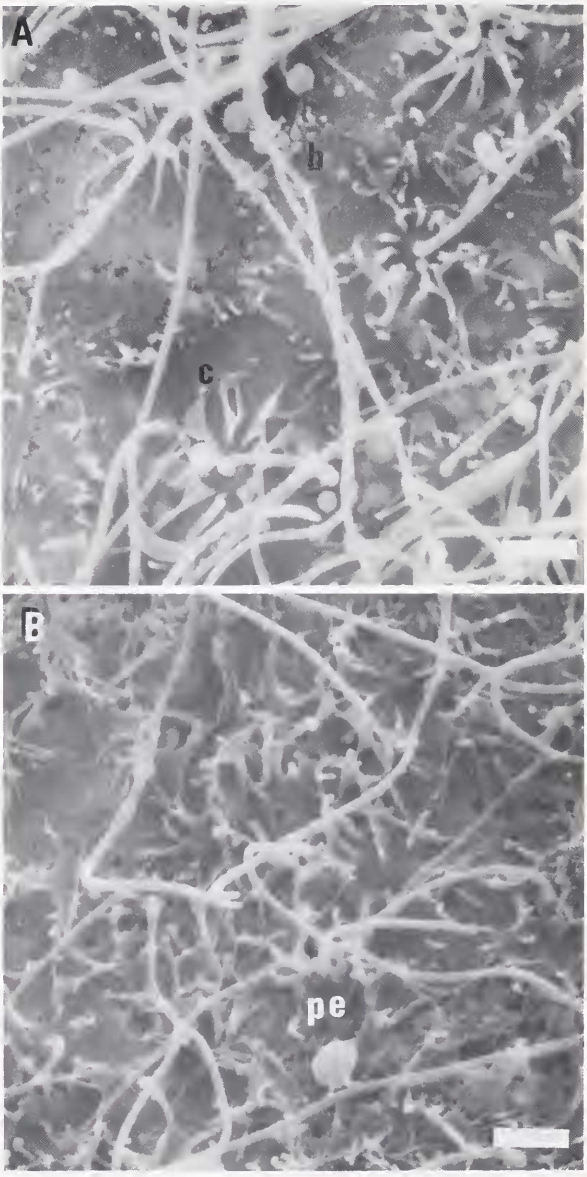

FIGURE 4. SEMs of endodermal cells, showing the surfaces of the membranes which face the coelenteron. Scale bar = 1.3 μm. a. Endoderm located in a gastrovascular pocket at the tip of the axial polyp; specimen fixed at 1500. Note circlet (c) of projections surrounding each flagellum and foreign particles, possibly bacteria (b) on the surface. b. Endoderm located in a gastrovascular pocket at the tip of the axial polyp; specimen fixed at 0500. Note the possible phagocytic event (pe). c. Endoderm located beneath outer ectoderm, 30 mm from branch tip. These cells contain zooxanthellae. Note the possible phagocytic event (pe).

b). In another case a mass of zooxanthellae plus some smaller objects (perhaps bacteria) were attached to the wall of a canal. In freshly collected coral tips, viewed with a 50× dissecting microscope, free zooxanthellae were observed in the peripheral canals at the tip of the branch.

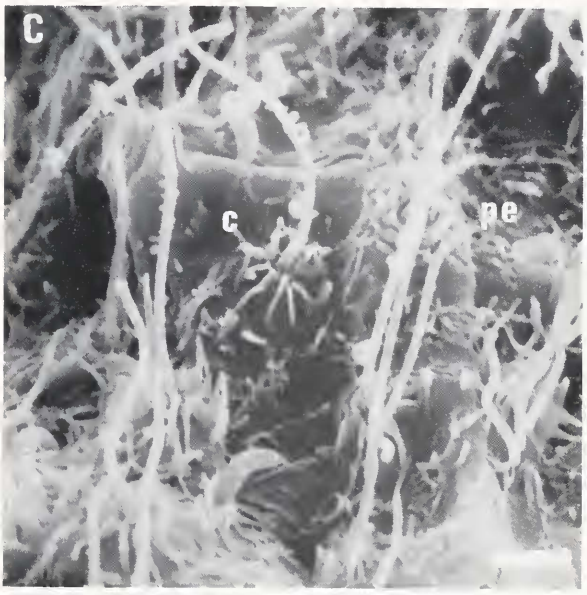

FIGURE 4. (*Continued*)

Patterns and rates of fluid transport

To detect the pattern and rate of flow in the gastrovascular system, fluorescein dye was injected into the system via a lateral polyp. Initially, just after the injection (t = 0), dye extended 0.7 cm proximally and 0.3 cm distally from the injected polyp. Usually the dye moved in both directions from the point of injection; distance traveled was measured each minute. The rate of movement was determined from the slope of a linear regression, plotting distance *versus* time; the coordinates at t = 0 were 0.7 cm for the proximal rate and 0.3 cm for the distal rate. In 75% of the trials the initial dye movement was in a right hand helical direction. The dye front moving proximally appeared fainter than that moving distally.

To determine if rate or pattern of flow was affected by distance from the branch tip, corals were injected at either 3 cm, 7 cm, or 10 cm proximal to the tip. To determine the effect of light on transport of fluids, some corals were maintained under daylight fluorescent light (750 ft candles), except during the 10 $s \cdot min^{-1}$ when the room was darkened to observe the position of the fluorescein visible under ultraviolet light. All determinations of the rate of transport as affected by distance from tip or by light were made between 1000 and 1500. The results of these experiments are shown in Tables II and III. The rate of flow was greater in the proximal direction than in the distal direction in 83% of the branches measured (Table II). This proportion is significantly different than expected if there were no difference in the rates in the two directions ($P < 0.005$, $\chi^2 = 92.1$). Table II also shows that neither light nor distance from tip affected pattern of flow, *i.e.*, proximal was greater than the distal rate.

Table III shows that rate of both proximal and distal flow was not significantly altered (as determined by *t*-tests between the means) by either distance from the tip or by the presence of light; *i.e.*, for each direction (*e.g.*, proximal) and each distance from the tip (*e.g.*, 3 cm) the dark value for rate (2.11 $cm \cdot min^{-1}$) is virtually the same

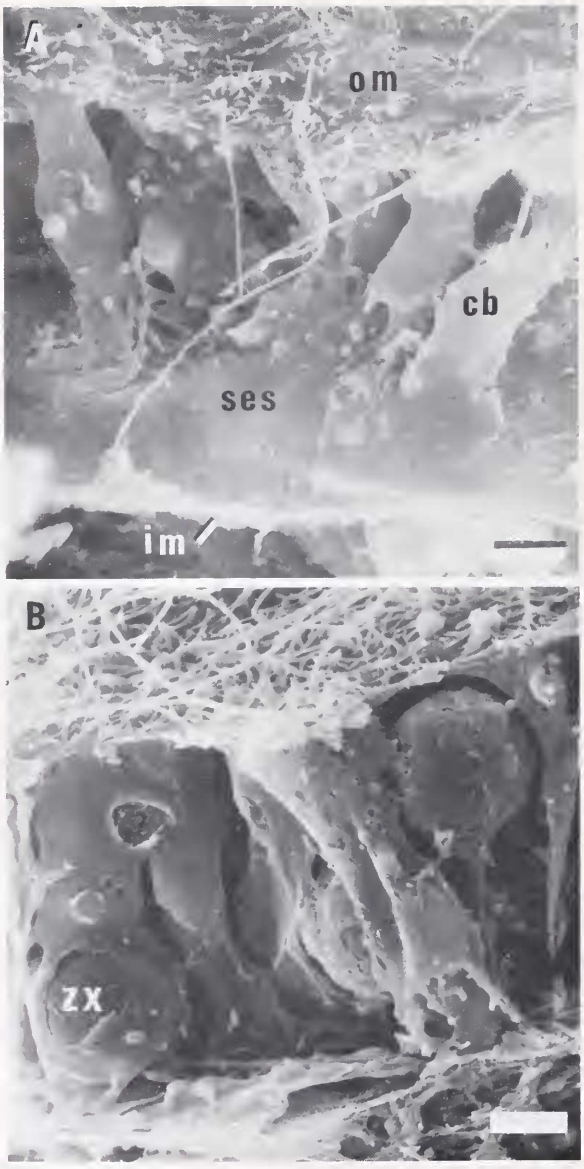

FIGURE 5. SEMs of endoderm: cross-section through the tissue layer exposing flagellated outer membrane surface (om) facing the coelenteron, body of the endodermal cells (cb), subepithelial space (ses), and inner membrane (im) adjacent to the mesoglea. Scale bar = 2.5 μm. a. Endoderm located in gastrovascular pockets near the tip of the axial polyp. The cells do not contain zooxanthellae. There is one flagellum per cell. b. Endoderm located adjacent to outer ectoderm 10 mm from the tip of the axial polyp. These cells do contain zooxanthellae (zx).

as the light value (2.10 $cm \cdot min^{-1}$) and the range of values in the proximal direction (1.72–2.14) found in the three distances from the tip are not statistically different. However, the mean rate of flow is significantly greater in the proximal than in the

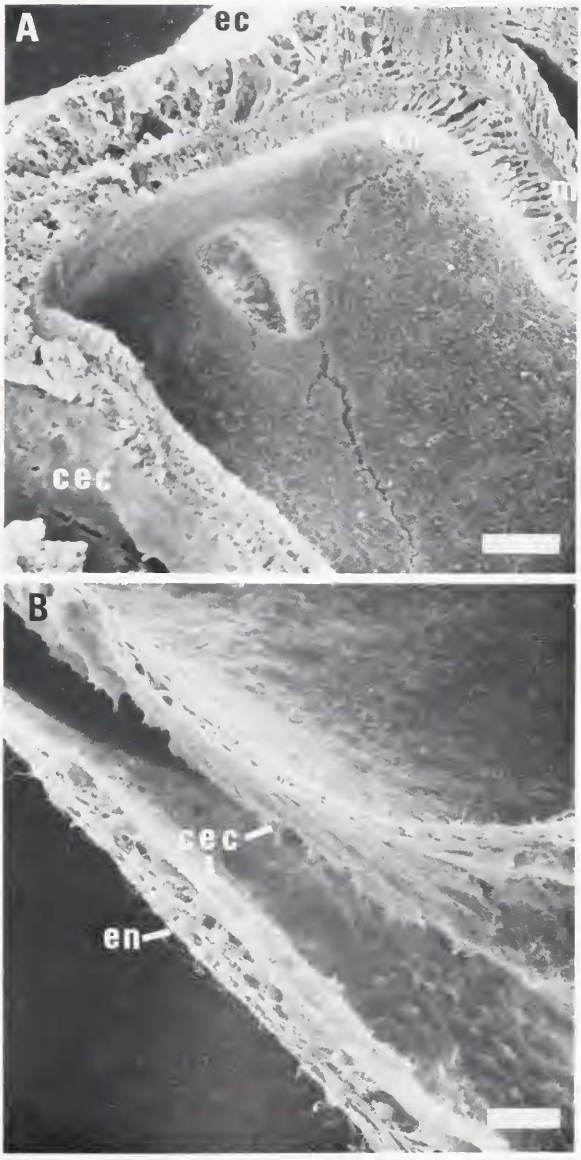

FIGURE 6. SEMs of longitudinal sections through a decalcified axial polyp, showing differences in morphology of endodermal cells from different locations. a. Gastrovascular pocket is located near the tip of the axial polyp with an opening to an adjacent pocket. Outer ectoderm (ec) covers the distal tip and is separated by mesoglea (m) from the calicoblastic ectoderm (cec) and endoderm (en). b. View *ca.* 300 μm from the tip showing the change in the shape of cells of the endoderm (en) and the calicoblastic ectoderm (cec) from columnar (see 7a) to squamous.

distal direction ($P < 0.001$, F = 43.51, ANOVA) under all conditions tested (Table III).

About 1 h after the termination of a series of measurements, the coral branches had expelled the fluorescein dye from all portions of the colony. The dye remained

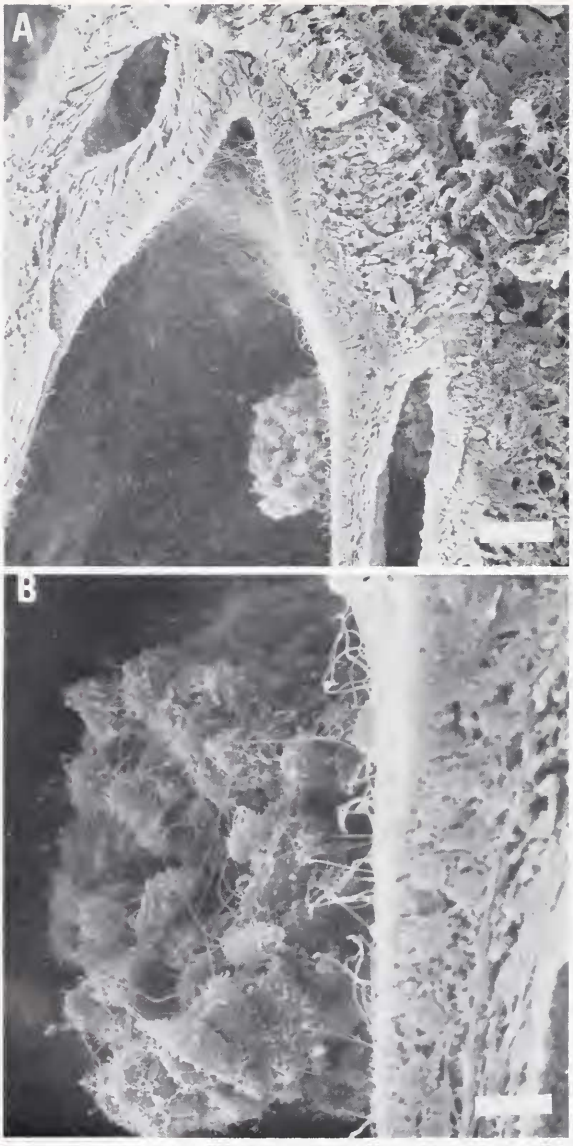

FIGURE 7. SEM of a decalcified axial polyp. a. A gastrovascular pocket located at the tip of the polyp. Note higher density of flagella towards the tip of the pocket. Also note the bolus of foreign material in the canal of the peripheral unit. Scale bar = 25 μm. b. Higher magnification of bolus in 7 a. Scale bar = 6 μm.

as a "cocoon" in the coral mucus surrounding each branch until the branches were rinsed and replaced in an aquarium with fresh flowing sea water.

To determine if rates or pattern of flow varied with time of day, one set of coral branches were monitored every 3 h, from 1200 on one day up to and including 1200 on the following day. A second set of corals were monitored *ca.* every 3 h from 1000 to the following 0130. The results are presented in Figure 8. The rate of fluid flow

TABLE II

Summary of the direction of fluid movement in the peripheral unit of individual branches[1]

Distance from tip (cm)	Dark (D) or Light (L)	No. of trials	Pr > Di		Pr = Di		Pr < Di	
			#	%	#	%	#	%
3	D	31	25	81	2	7	4	13
	L	13	10	77	2	15	1	8
7	D	21	17	82	1	5	3	14
	L	5	5	100	0	0	0	0
10	D	5	4	80	1	20	0	0
	L	26	22	85	3	12	1	4
Total no. trials		101	83		9		9	
% of total trials				83		9		9

[1] Data presented are the number of trials in which the rate of movement of the dye front was greater in a preferred direction (*i.e.*, distal, Di or proximal Pr) or equal in both directions (within 0.1 cm · min^{-1}).

in the proximal direction was always greater than that in the distal direction, confirming the results presented above. There was, however, a diel pattern in the rate of fluid transport. Highest rates occurred between 2400 and 0900, with a rapid decline in the rate of flow at mid-morning to the low between 1000–1200 until about 1800 when the flow rates began a gradual increase to the early morning peak.

No movement of fluid occurred in the control branches which had been fixed in formalin.

All measurements of fluid transport described above refer to observations of dye moving in an axial orientation (either proximal or distal) just beneath the surface of the outer ectoderm of the colony. To determine the rate and direction of fluid movement in the axial core of a branch, several approaches were taken. The first was to observe the time at which dye injected into a lateral polyp was first observed in the proximal portion of the axial polyp exposed on the open portion of a branch. The second approach involved directly injecting the axial polyp and noting the time at which the dye reached the proximal end of the axial polyp. Finally the distal tip (*ca.* 2 cm) of a coral branch injected either via a lateral polyp or via the proximal end

TABLE III

Rate of fluid movement (cm/min) in peripheral canals in the proximal (Pr) and distal (Di) direction as affected by distance from branch tip and illumination (L, light; D, dark)

Distance from tip (cm)	Dark (D) or Light (L)	Proximal			Distal		
		$\bar{x}$	S.D.	n	$\bar{x}$	S.D.	n
3	D	2.11	0.64	30	1.35	0.54	31
	L	2.10	0.78	14	1.58	0.74	13
7	D	1.72	0.82	21	1.02	0.44	20
	L	1.90	0.80	5	1.05	0.21	5
10	D	2.14	0.56	5	1.28	0.40	5
	L	2.08	0.71	26	1.37	0.33	26

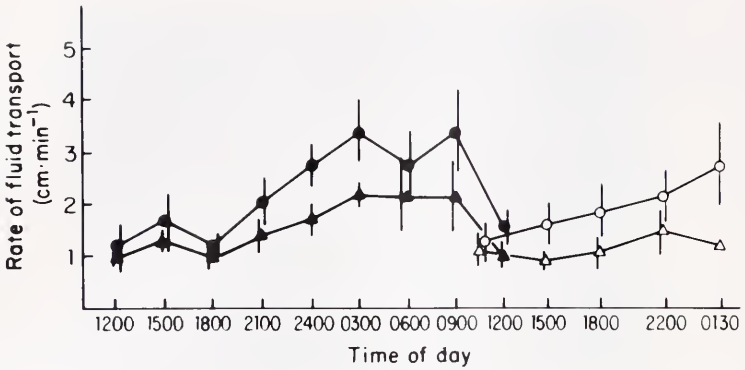

FIGURE 8. Diel patterns of the rate of fluid movement in the peripheral unit of the gastrovascular system. Each point represents data from 12 coral branches; closed points are from the second set. Values plotted are the mean of 12 measurements and the 95% confidence limits. Proximal flow is indicated by circles; distal flow is indicated by triangles.

of the axial polyp was broken so that dye moving distally in the axial polyp could be detected. The results of these investigations are summarized in Table IV. Dye injected into either the axial polyp or a lateral polyp was first observed at the center of the broken proximal end of the branch (in the axis) and later at the edges (*i.e.*, circumference) of the proximal end of the branch. Fluid transport in the distal direction in the axial canal was never observed. Rate of fluid conduction in the axial canal was always 2–3 times greater than the rate of fluid transport just beneath the outer ectoderm. Dye was never seen in the area between the periphery and the axis, indicating that the canals in this area served mainly for radial conduction of fluids. Some of the dye injected into a lateral polyp is transported to the axial polyp, and some of the dye injected into the axial polyp is transported to the periphery.

TABLE IV

Summary of rate and direction of fluid movement in the axial canal

n	Position of injection	Position of dye after transport	Rate (cm · min^{-1}) $\bar{x}$	S.D.
5	axial polyp (distal)	axial canal-proximal end	11.4	10.7
		peripheral canal-proximal end	rate not measured, but dye present	
5	axial canal (proximal)	axial canal-distal end	NEVER observed	
		peripheral canals	1.9	0.6
17 tips*	lateral polyp, 5 cm from tip	axial canal-distal end	NEVER observed	
		axial canal-proximal end	6.5 range (3.4–9.9)	2.2
		peripheral canals	see Figure 8 range (1–3)	

* 74 trials.

Discussion

The fluid transport system of *Acropora cervicornis* consists of the canals of the gastrovascular system. These canals conduct fluids axially along a branch and radially between the periphery and axis of the branch. Two units, peripheral (P) and axial (A) are responsible for conduction along the axis of a branch. The peripheral unit consists of small peripheral canals. It conducts fluid proximally and distally. The axial unit consists of the large axial canal. It differs in two respects from the peripheral unit: 1) flow is always in the proximal direction and 2) the rate of flow is 2–3 times greater. The peripheral and axial units are connected by a radially conducting unit consisting of the canals of the lateral polyps and smaller short canals within the radial secondary growth of the skeleton. This radial unit can conduct fluids both towards and away from the branch axis. Fluid moving from the outside medium into the gastrovascular system was never directly observed. The "cocoon" of mucus with expelled dye which surrounds the entire coral branch *ca.* 1 h after the injection of the dye suggests that exchange of gastrovascular fluid with the outside medium occurs via all the lateral polyps and perhaps the axial polyp as well.

The mechanism of fluid propulsion is probably flagellar action. Musgrave (1909) described a ciliated canal system in a pennatulid, and suggested that it functioned in intracolonial transport of fluids. Parker (1920) observed that circulation in *Renilla* followed a specific route. Thus, the idea of a circulatory system in colonial cnidarians, with fluid propelled by cilia has been in the literature for a number of years. In *A. cervicornis* the flagella are short (10–15 μm) like cilia, but since there is only one per cell, the conventional terminology employed by Robson (1957) will be used in this discussion. In references to past literature, when the term "ciliated canals" is used, I will refer to the tubules in that form.

The fluid transport system operates under low Reynolds numbers; the Reynolds number of the axial transport unit (A) and the peripheral unit (P; and p, for one canal in the unit) can be calculated (Alexander, 1968):

$$\mathrm{Re} = \rho u a/\eta$$

where

ρ = density of fluid

u = velocity of fluid

a = radius of canal

η = viscosity of fluid; and

$\eta/\rho = \nu$ = kinematic viscosity = $10^{-2}\ \mathrm{cm^2 \cdot s^{-1}}$

$u_A = 10^{-1}\ \mathrm{cm \cdot s^{-1}}$; $u_P = 3 \times 10^{-2}\ \mathrm{cm \cdot s^{-1}}$

$a_A = 5 \times 10^{-2}$ cm; $a_p = 5 \times 10^{-3}$ cm

so that

$$\mathrm{Re_A} = 5 \times 10^{-1} \text{ and } \mathrm{Re_p} = 1.5 \times 10^{-2}.$$

Since a Reynolds number of >2000 is necessary to produce turbulent flow (Vogel, 1981), the fluids in the gastrovascular system of *A. cervicornis* have a laminar flow.

Roosen-Runge (1967) described a very similar system in the circulation of fluids in the canals of a small hydromedusa, *Phialideum* sp. He observed rates of flow *ca.* 100 $\mu\mathrm{m \cdot s^{-1}}$ in canals with radii of 25 μm. Using these values and the Poiseulle equation he concluded that the circulatory system of the medusa was operating at pressures of .12 mm-Hg. Unfortunately, Poiseulle's equation cannot be applied in a

situation in which fluid is propelled by flagella because Poiseulle's equation depends on a pressure differential and assumes that "the fluid velocity at the edge of the tube is zero" (Feigl, 1974). In ciliated tubes the "pump" is located all along the length of the tube and the flow velocity profile is reversed from that seen in Poiseulle flow (Vogel, 1981). A fluid flow profile normal to a ciliated wall shows a maximum velocity *ca.* 2 cilia lengths from the ciliated wall with a decrease in velocity to zero at 10 cilia lengths from the ciliated surface (Cheung and Winet, 1975). In a tube lined with cilia, each of whose length is 20% of the radius of the tube, the flow velocity profile is almost flat due to the combined effect on water particles from cilia located on opposite sides of the tube (Gray, 1928). A peripheral canal of *Acropora cervicornis* presents such a situation. The length of a flagellum is *ca.* 25% of the radius of the canal. In fluid flow along this type of canal, the most important force is tangential, the wall shear stress (Brennan and Winet, 1977). Descriptions of fluid flow in ciliated tubes have largely been confined to mucociliary systems. Even in these accounts there are not enough sufficient observations or quantitative information to adequately describe the hydrodynamics of flow (Brennan and Winet, 1977). Perhaps the two dimensional model, Couette flow (R. Kelly, pers. comm.), describing a wall moving in relation to a fluid in which tangential force is the most important component affecting the velocity profile, is most applicable.

In the axial canal of *A. cervicornis,* flow induced by flagellar beating would produce a flow velocity profile decreasing from a maximum velocity 2 flagellar lengths from the wall to a velocity of zero at 10 flagellar lengths from the wall. If flagella are the only propulsive force, then fluid in the center of the axial canal would be stationary, since 10 flagellar lengths is equal to about 130 μm from the wall while the radius of the axial canal is 500 μm. Whether the central fluid is stationary or whether some other force moves this fluid cannot be ascertained from this study.

In the canals of the medusa, *Phialidium* sp. (Roosen-Runge, 1967), muscular action could affect the direction, and sometimes the rate of flow, but the flagella were the main driving force. Brafield (1969) concluded that in the pennatulid, *Pteroides* sp., the peristaltic muscular contractions were the most important driving force in the circulation of fluids throughout that colony. In *Acropora cervicornis,* muscular action probably plays no role because the canals of the gastrovascular system are set at a fixed size due to their position, embedded in a rigid skeleton.

In Roosen-Runge's study (1967) he observed the actual movements of particles within the canals and he was able to discern that flow could proceed in opposite directions in the same canal. This might provide an explanation for the observation that the peripheral unit of *A. cervicornis* can carry fluids in two directions at the same time. In an analysis of a stationary protozoan, Cheung and Winet (1975) found flow velocity profiles showing a backflow of fluid between a ciliated wall and up to 0.5 cilia lengths from the wall, with the maximum forward velocity occurring at 2 cilia lengths from the wall. If this pattern occurs in a peripheral canal of *A. cervicornis,* it could be the mechanism by which flow could proceed in the opposite direction in the same tube. In systems operating under low Reynolds numbers, such as cnidarian circulatory systems, the fluids act very viscous. Consequently, very little mixing of adjacent streams need take place (Vogel, 1981). In these peripheral canals, a large surface area relative to that of the axial canal, presents a site for exchange of dissolved and particulate matter. The cell membranes of the endodermal cells lining the peripheral canals are often highly folded, and phagocytic events can be observed in SEMs.

Pearse and Muscatine (1971) and Taylor (1977) demonstrated that soluble organic molecules and inorganic ions are transported distally to the growing tip of *Acropora*

cervicornis. Other investigators found that only after a short time (30 min) can radioactive food fed to a colonial cnidarian polyp be detected in adjacent polyps (Rees *et al.*, 1970; Murdock, 1978a, b). Furthermore, Rees *et al.* state that in a growing hydroid colony, "radioactive food fed to the terminal hydranth seemed to be preferentially utilized by the growing regions." Thus, it is not surprising that the growing tip of *A. cervicornis* (*ca.* 300 $\mu m \cdot day^{-1}$; Gladfelter, 1982) serves as a "sink" for soluble organic material and Ca^{++}, required for the development of the axial polyp and the skeleton (Pearse and Muscatine, 1971; Taylor, 1977). The role of the gastrovascular system in removing materials from the growing tip has not been investigated. Several hypotheses to explain light enhancement of calcification depend on the removal of substances from the sites of crystal deposition (*e.g.*, Goreau, 1959; Simkiss, 1964; Gladfelter, 1983); the role of the fluid transport system in effecting removal of materials is unknown.

To resolve some of the questions concerning calcification it would be useful to know the chemical properties of the fluid in the gastrovascular system. Obviously, most useful would be data on the chemical composition of fluids outside the calicoblastic ectoderm, *i.e.*, just adjacent to the developing skeleton, but these data are extremely difficult to obtain, even in relatively large volume reservoirs such as the extrapallial fluids of molluscs (Simkiss, 1982). Additionally, it would be useful to know the rate of exchange of fluids between the gastrovascular system and the external medium. On one hand, if the gastrovascular system serves to distribute soluble organic matter throughout the colony to sites which can use it as an energy source or as precursor molecules, it would be disadvantageous to rapidly exchange the gastrovascular fluid for sea water. The zooxanthellae can serve to clean the system of metabolic wastes, as they effectively remove ammonia (Muscatine, 1980) and probably other materials as well. However, at some point, the fluid in the gastrovascular system would become depleted of such things as calcium ions, which the colony needs for extension of its skeleton as well as increasing the strength of the skeleton by subsequent infilling of pores (Gladfelter, 1982).

To summarize, the gastrovascular system of *Acropora cervicornis* serves as a circulatory system, characterized by: (1) two units (axial and peripheral) conducting fluids by means of flagella along the axis of the branch; (2) a low Reynolds number, leading to laminar flow; (3) a predictable diel pattern in the rate of flow in the peripheral unit; and (4) no change in the rate of flow due to light.

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